THE DEVELOPMENT OF AGARICUS ARVENSIS AND A. COMTULUS[1]

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The development of *Agaricus campestris*[2] from the very young and undifferentiated carpophore was published in 1906. In 1905 young carpophores of several species of agarics in different stages of development were collected in the forests of the Jura Mountains in the vicinity of Pontarlier, France, during a three weeks' sojourn at that place. Among these were *Agaricus arvensis* Fr., and *Ag. comtulus* Fr.

MATERIAL AND VERIFICATION OF SPECIES

The material for the study of *Agaricus arvensis* was collected in a dense spruce forest, to the north of Pontarlier, maintained by the city government. The young carpophores were found in the forest mold in connection with the mycelium of a large plant which was not quite mature, *i. e.*, not fully expanded. The large immature individual was taken to my provisional laboratory in the hotel, photographed before the rupture of the veil, and then kept for a day or two for photographing in the fully expanded state. There may be some question as to whether this plant is *Agaricus arvensis* or *Agaricus xanthodermus* Genev. (= *Ag. flavescens* Roze, not *Ag. flavescens* Gillet). Other plants collected in the same forest, and communicated to M. Emile Boudier, of Montmorency, near Paris, were determined as *Ag. xanthodermus*. The single plant from the same mycelium as the young carpophores could not well be sent to M. Boudier since it was immature when collected and it was desirable to keep it until expanded for the purpose of photographing it.

The important characters of the plant noted at the time are as follows: Pileus and stem pure white, pileus smooth or with very fine appressed scales. Veil thick, ample, slightly cracked radially at the margin and with regular, angular scales on the under side of the margin. The flesh remained unchanged where bruised, and the surface of the

[1] Investigation prosecuted with the aid of a grant from the Botanical Society of America in 1905.

[2] Atkinson, Geo. F. The development of *Agaricus campestris*. Bot. Gaz. **42**: 241–264 *pls. 7–12*. 1906.

pileus did not yellow to the touch, perhaps due to the fact that the plant was collected young and then kept for a few days under unnatural conditions. The flesh of the stem was not yellow at the base which is said to be a character of *Ag. xanthodermus*. There was a slight odor of almonds, which is present, however, in several species of *Agaricus*.

This forest form described above (no. 21054 of my collections) is quite different in appearance from the robust form which occurs in pastures in the Jura Mountains. It is almost impossible to obtain full grown forms of these robust specimens in the vicinity of Pontarlier, since they are much prized as edibles and the localities where they are known to occur are visited almost every day by collectors who take them in the young stage soon after their emergence from the ground. On a hillside of a pasture northeast of Pontarlier there is a large arc of a fairy ring which is probably several centuries old. If the circle of this arc were completed its diameter would be several kilometers. M. August Dornier, of Pontarlier, in whose house I lived during my stay in 1910, informed me that during the past 25 years he had collected *Agaricus arvensis* each year from this same arc of a fairy ring. It is a long arc with a slight but gradual curvature, and is quite conspicuous on the hillside because of the dark green color of the grass.

I collected several young plants from this ring on August 8, 1910. They were quite robust and were just beginning to expand. They were carried to my room, transplanted into pots of earth, covered with a bell jar and photographed August 10 and 11. The removal from the earth checked their development.

Although they opened so that fair photographs were obtained, the plants did not reach their full size. Notwithstanding this, the pileus of the largest measured 12 cm. in diameter and the stems 3–5 cm. thick. The pileus was white, then gray and very scaly at maturity with fibrous appressed scales, many of them upturned toward the margin. Bruises of the surface of pileus and stem change slightly to yellow or pale saffron. The veil is large, thick, very floccose below and radiately split into coarse scales toward the margin, those on the edge being tinged with gray. The stem is smooth above the annulus but very scaly below, with larger conic scales crowded near the base and often in concentric rings. In age these large scales become dull pale brown, while upward they grade into smaller and lighter colored ones, the uppermost, next the annulus being floccose

and white. There was a faint odor and taste of almonds. M. Boudier, to whom specimens were sent, confirmed the identification as *Ag. arvensis*. It is therefore a peronate variety of *Agaricus arvensis* comparable with *Agaricus perrarus* Schulzer,[2] which is considered by some to be a form of *Agaricus augustus* Fr. Similar forms of *Agaricus subrufescens* Peck[3] are sometimes found, which perhaps are identical with *Ag. perrarus* Schulz. while the normal forms of *Ag. subrufescens* Pk. are very near to *Ag. augustus* Fr., and this *Ag. subrufescens*, perhaps, may be considered a slender, small-spored variety of *Ag. augustus*.

Another form intermediate between this strongly peronate form of *Ag. arvensis*, and the forest form (no. 21054), was found not far from the fairy ring described above. This (no. 24763) plant was growing in the edge of a small clump of bushes and small trees situated in the pasture, and was fully expanded. It was 20 cm. high, the pileus 15 cm. broad and the base of the stem 4 cm. thick. The pileus was white, smooth or with delicate appressed scales. The annulus was large, membranous, and the under surface with large regular scales near the margin, radiately arranged. The stem was smooth, at first white, then later slightly rufescent and minutely scaly over the upper part of the fusoid bulb or base. There was a slight odor and taste of almonds.

Agaricus arvensis is therefore quite variable in the Jura Mountains according to location and other conditions. A number of different varieties of *Agaricus arvensis* are recognized by some authors, though there will probably always be differences of opinion as to the limits of this and related species, because of their great variability, and because of different opinions as to the concept of species. But it seems quite reasonably certain that the material from which this study of development is made belongs to a forest form of *Agaricus arvensis*.

DEVELOPMENT OF AGARICUS ARVENSIS

Primordium of pileus, stem and hymenophore

Early differentiation of the interior of the carpophore.—Fruit bodies 2.5 mm. long by 2 mm. in diameter show a faint differentiation of the internal portion into pileus and stipe fundaments, but the peripheral

[2] Verhand. K. K. Zool. bot. Ges. —: 493. 1879. See also Bresadola, J. Fungi Trid. 1: 54. *pl. 89.* 1887.

[3] Described in 6th Rept. N. Y. State Mus. Nat. Hist. 25. 1893.

portion of the carpophore stains more deeply. The hyphae of the peripheral portion have somewhat thicker walls and less protoplasmic content than those of the interior, *i. e.*, of the pileus and stem fundaments. The walls of these hyphae are well stained with the haematoxylin, and this portion contrasts rather clearly with the interior because it is more deeply stained and also because the meshes of the tissue are somewhat larger. The features which mark the differentiation of the internal portion into pileus and stem are the very slight indication of the annular gill cavity, the appearance of a constriction between the stem and pileus fundaments, and the abrupt narrowing of the internal portion, so that the pileus primordium appears as a small round projection from the broader basal portion, the primordium of the stem. The looser, more deeply staining tissue surrounding the pileus and stem primordium is fundamental tissue, the outer portion of which may be regarded as the "universal veil," though its inner limits cannot be clearly defined.

On the exterior the young carpophore does not yet show any constriction because the enveloping zone of fundamental tissue has not yet become subject to distortion from the internal changes of form. This condition exists until some time after the origin of the primordium of the hymenophore, when the expansion of the pileus becomes greater than the lateral expansion of the stem, and an external constriction is then evident.

The hyphae of the interior portion of the very young fruit body are 3–4.5μ in diameter, have very thin walls, and the rather scant cytoplasm alone appears to be stained.

Character of the pileus primordium.—The annular gill cavity is formed by the more rapid growth and extension of the surrounding tissue. It appears between the margin of the pileus and the stem fundaments. The absence of a more deeply staining central portion in the upper part of the young fruit body contrasts strongly with the condition in *Hypholoma* described by Miss Allen,[4] in *Lepiota clypeolaria*,[5] and with the condition described by Fayod[6] as the rule for the Agaricaceae. It agrees with the condition found by myself in *Agaricus*

[4] Allen, Caroline L. The development of some species of *Hypholoma*. Ann. Myc. **4**: 387–394. *pls. 5–7*. 1906.

[5] *Lepiota clypeolaria* will be described in another paper.

[6] Prodrome d'une histoire naturelle des Agaricinés. Ann. Sci. Nat. Bot. VII, **9**: 181–411. *pls. 6, 7*. 1889.

campestris,[7] except that in the specimens of the latter species studied there was no morphological differentiation of the fundamental tissue indicating the pileus and stem fundaments distinct from the surrounding fundamental tissues, as in *Ag. arvensis*, until some time after the first evidence of the hymenophore primordium. In the young fruit bodies of *Agaricus campestris* examined, there appears an annular region of more deeply staining hyphae before any evidence of the annular cavity is seen, and just above the region where this is formed.

Median longitudinal sections of these very young carpophores of *Agaricus arvensis* show that the hyphae in the pileus primordium have in general a radiate direction. But the central ones show this character only in a slight degree, the hyphae are much interwoven and over the central area where the pileus primordium passes over into the external fundamental tissue they are intricately interwoven, no radial direction is evident and they show no evidence of specially active growth.

The lateral hyphae, however, show distinctly a radial direction and curve outward at the same time somewhat like the lateral stalks in a sheaf. The outer and lower ones curve more strongly, and the terminations of the lower ones curve downward next the outer fundamental tissue and directly above the looser mesh where the annular gill cavity is forming. These hyphae stain more deeply than the remaining elements of the pileus primordium, but the contrast is not very striking, and they lie very close to the external fundamental tissue which is deeply stained. Consequently this primordium of the hymenophore and pileus margin is not differentiated in the photograph of the entire section, figure 1. But in figure 8 more highly magnified, it can be seen that just above the more open mesh there is a narrow area next the external fundamental tissue where the hyphae compacted together have a downward direction. The external fundamental tissue presents a very distinct texture since the walls of the hyphae are thick and the mesh is open though not so open as that where the gill cavity is forming.

The primordia of the hymenophore and of the pileus margin are merged in the early stages.—In slightly older stages, as shown in figure 2, the gill "slit" is distinct though narrow, and the primordium of the hymenophore is very distinct, not only by the deep stain of the

[7] Atkinson, Geo. F. The development of *Agaricus campestris*. Bot. Gaz. **42**: 241–264. *pls. 7–12.* 1906.

tissue, but by the parallel course of the crowded hyphae, which now form a more extensive area. The primordium of the pileus margin into which the hymenophore merges is also distinct. The hyphae are parallel and epinastic. It can be seen here, and in still older carpophores, that the radial and parallel arrangement of the hyphae, and their deeper stain, progresses centripetally, *i. e.*, toward the center of the upper surface of the young pileus. This is brought about because successive areas in the same direction in the pileus primordium gradually assume active growth, new hyphae are formed in abundance which extend radially, and curve downward under the influence of epinasty. The advance hyphae penetrate through the fundamental tissue. Some of them can be seen to grow into the inner portion of the external fundamental tissue.

Character of the hyphae in the young hymenophore primordium.— Here, as described for *Agaricus campestris*, many of the earlier hyphae of the young hymenophore primordium are very slender and sharp-pointed. This form permits them more easily to make their way through the tissue until they reach the annular cavity. When the sharp-pointed hyphae are exposed in the annular cavity, their form soon changes, or the new elements developed are different in form. The hyphae are now short, blunt at their free ends and form a very compact palisade layer. As centrifugal growth of the pileus continues at the margin, the new elements arise in the same order as the gill cavity is extended. The newer elements growing into the cavity are sharp-pointed and often crowded into an uneven palisade layer, but the transition to the blunt palisade cells is soon effected.

In figures 1–3, the youngest carpophores studied, the internal portion immediately below the constriction, and the annular cavity, is more deeply stained than the pileus primordium and the basal part of the stem. This activity of the hyphae in this region seems to be connected with the primordial differentiation of the stem. This can be traced in the older carpophores as seen in figures 2, 3 and 5, where the demarcation of the stem surface gradually appears. The stem in the very young fruit bodies is thus seen to be very short, its breadth exceeding its length for some time. The tissue marking the outline of the stem is thus more active and stains more deeply than that of the pileus, except in the immediate region of the hymenophore, and the margin of the pileus, where growth and the formation of new hyphal elements is necessarily active.

It is interesting to observe that during the early growth of the young hymenophore, and of the gill cavity, their outline rises from the point next the stem at an oblique angle outward and upward. Epinastic growth of the hyphae in the margin of the pileus begins early so that the hymenophore at this point curves outward and downward over the upper angle of the gill "slit." As the fruit body enlarges, continued epinasty tends to move the whole pileus margin downward while the extreme margin is inrolled. At the same time elongation of the stem begins which tends to carry the inner angle of the gill slit and the hymenophore upward, so that the angle at which they formerly stood is reversed and they extend outward and downward.

Origin of the partial veil.—Since the hymenophore is endogenous in origin, the partial veil originates from the fundamental tissue lying outside the annular cavity and is not clearly separated from the universal veil. It is thus connected with the margin of the pileus and the surface of the stem. This fundament of the annulus, or partial veil, increases in extent by tension resulting from the expansion of the pileus and stem, and also by growth of the elements, which growth, however, does not keep pace with that of the surrounding parts. In the older fruit bodies, as shown in figures 5 and 6, this veil is duplex in structure. The lower portion lying next the stem surface has a looser texture, is the principal aerating tissue, is derived from fundamental tissue and increases by growth of its elements. The upper portion lying next the gill cavity is connected directly with the margin of the pileus. It originates partly from fundamental tissue and partly by growth from the margin of the pileus, the growth from the pileus probably forming the denser portion. The lower looser portion is torn off from the surface of the stem during further growth and expansion of the plant, and provides the looser lower portion of the duplex veil characteristic of *Agaricus arvensis* and some of the other species of *Agaricus*, like *Ag. augustus* Fr., etc. Its looser texture would permit of its being torn into angular, often radiating areas or patches, so striking a feature of the duplex veil of these species. In very robust specimens the increase in the fundamental tissue between the partial veil and stem appears sometimes to be very great and this very likely provides the looser tissue which forms the floccose scales on the stem below the annulus in the peronate forms.

DEVELOPMENT OF AGARICUS COMTULUS

Primordia of pileus, hymenophore and stem.—The youngest fruit body of *Agaricus comtulus* Fr. sectioned was 1.25 mm. long by .75 mm. in diameter. This shows the earliest stages of the primordium of pileus, stem and hymenophore, before there is any indication of the annular gill cavity. In longitudinal section the primordium of the hymenophore appears as two dense, deeply staining, rounded areas, symmetrically located on either side of the axis and some distance below the surface, showing that it is also endogenous in origin. The pileus primordium above is indicated by a very faintly staining dome-shaped area. Below, the stem primordium is indicated by a more densely staining area, distinct in this respect from the lighter staining basal area in which the tissue is of a looser texture.

Character of the external zone of the young carpophore.—Above the pileus primordium, and lateral to the hymenophore, the tissue is of a much looser texture, the hyphae in general having a radial arrangement but flexuous and intricately interwoven with adjacent ones forming a loose mesh work, not at all comparable to the palisade layer of radial hyphae enveloping the upper part of the carpophore in *Lepiota clypeolaria*, *Armillaria mellea*, etc.

Later stages of organization.—In the next stage examined the fruit body was 5 × 3 mm. The fundamental parts of the fruit body are well advanced and the external constriction marks the limit of pileus and stem. The gill cavity and hymenophore are already evident (figure 10). The rudimentary hymenophore is furnished with the palisade layer of blunt cells. The tissue which forms the partial veil, lying between the annular gill cavity and the outside is already of much looser texture, the lower portion of a much more open mesh, while the upper portion next the hymenophore or gill cavity is more dense as described above for *Ag. arvensis*.

In figure 11 is represented a much older fruit body where gill formation has already reached quite an advanced stage. The outline of the stem surface is very clearly shown. The duplex character of the veil is very striking with its looser texture below and the denser portion above. The further stages of its development are as usual.

THE UNIVERSAL AND PARTIAL VEILS IN AGARICUS

In the three species of *Agaricus*, which I have thus far studied, the hymenophore is of deeper origin than that of *Psalliota rubella*

(*Agaricus rubellus* Gillet) as figured by Fayod[8] (l. c., *pl. 7.* fig. 4) which he places in his subangiocarpous type ("*type subangiocarp.*" pp. 284, 285) to which he says the majority of the species of *Psalliota* (*Agaricus* as limited here) probably belong. In this type, according to Fayod, the universal veil is not differentiated from the cuticle of the pileus but remains concrete with the pileus as stated by Fries[9] for the species of his Tribe *Lepiota*. In the subangiocarpous type Fayod interprets the universal veil (voile generale) to include the partial veil, the outer layer of the carpophore continuous with the partial veil, together with the fundamental tissue which separates from the stipe. It would include the outer zone of the mature pileus, since the universal veil, according to this interpretation, does not separate from the pileus but remains in intimate union with it.

A primary universal veil in Agaricus campestris.—In *Agaricus campestris* there is often formed a well differentiated, but delicate and floccose, universal veil,[10] quite distinct from a very young stage, which at maturity separates distinctly from the surface of the pileus. It is as strongly developed as the universal veil which is present in *Pholiota caperata* on which Karsten based his genus *Rozites*.[11] But in this species there is a definite pileus cuticle or cortex of specialized cells, forming a clear and distinct differentiation from the universal veil. In *Agaricus* the cuticle of the pileus is fibrous and not specialized. In other species of *Agaricus* a similar delicate universal veil is sometimes present. What I have heretofore regarded as the universal veil in *Agaricus campestris* is this outer layer of loose fundamental tissue. It is a primary universal veil, evident on the young carpophore, and which can be seen in sections at later stages as a thin loose layer enveloping pileus and partial veil, though not separated so cleanly from the carpophore as in the genus *Amanita* where the universal veil is usually much stouter, and not strictly homologous with the freed portion in *Agaricus campestris*.

Organization of pileus surface.—In no one of the three species of *Agaricus* which I have studied does the pileus surface, during its

[8] Prodrome d'une histoire naturelle des Agaricinés. Ann. Sci. Nat. Bot. VII. **9**: 181–411. *pls. 6, 7.* 1899.

[9] Syst. Myc. **1**: 19. 1821.

[10] Atkinson, Geo. F. The development of *Agaricus campestris*. Bot. Gaz. **42**: 241–264. *pls. 7–12.* 1906.

[11] Karsten, P. A. Rysslands, Finlands och Skandinavikar Holfäns Hattsvampar. **1**: 290. 1879.

early organization, stand out so distinctly from the enveloping tissue as is shown in the illustration of *Agaricus rubellus* by Fayod.[12] Although, in some cases it appears that the primordium of the pileus, in the form of an internal area, central in the upper part of the carpophore primordium, may be distinguished from the surrounding tissue, slightly before or simultaneous with the earliest appearance of the hymenophore primordium (see figure 4) by the more active growth of the hyphae, and consequently the deeper staining of this area, the hyphae are intricately interwoven and show no organization into a definite structure. The earliest differentiation which indicates the organization of a structure, in the three species which I have studied (*A. campestris*, *arvensis* and *comtulus*), is marginal, and is the primordium of the hymenophore. Since it is impossible in very young stages to clearly distinguish between the hymenophore and pileus margin, this early marginal growth may share in the organization of both structures. Epinastic growth is first manifested in this marginal region, and, simultaneous with the progressive development of the hymenophore, epinasty is more and more marked.

Organization of the primordial surface of the pileus.—The organization of the pileus structure, judged by the radial and epinastic growth of the hyphae, and the clearness with which it can be differentiated from the external fundamental tissue, is marginal also. While it is not separated from the external fundamental tissue, the parallel, radial and epinastic direction of the hyphae enables one to distinguish it quite clearly from the interwoven texture of the external fundamental tissue. From this point the organization of the pileus cortex seems to proceed to some extent in a centripetal direction, but the region over the center is very limited in such young specimens and the hyphae of course do not grow from the marginal area toward the center. Successive areas of the primorial tissue of the young pileus surface, in a centripetal direction, organize new and abundant hyphae which grow in a radial direction, and become curved downward by epinasty. The subsequent development of the pileus is for the most part centrifugal.

Fundament of the universal veil.—In figures 1–4 of *Agaricus arvensis*, and figures 7 and 10 of *Ag. comtulus*, external to the fundaments of

[12] Also the structure of the universal veil as figured by Fayod for *Agaricus rubellus* is very different from anything which I have seen in the species of *Agaricus* which I have studied.

the pileus and stem is a broad zone of fundamental tissue characterized by a more open mesh. It has already been noted that this tissue is composed of thick-walled hyphae quite distinct from the thin-walled hyphae of the denser inner tissue, though at the border between the two there is more or less a merging of both elements. This zone of tissue is homologous with that in *Amanitopsis vaginata* which forms the volva or universal veil. In the young carpophores of *Amanitopsis vaginata* there is a similar loose-meshed tissue surrounding the primordium of pileus and stem which merges gradually into the denser tissue within, and which only at a later period is separated as the volva, by a zone of gelatinizing hyphae. This universal veil while still undifferentiated may be called the *blematogen*,[13] or *blematogen layer*, yet unfashioned as a volva.

Relation of partial veil, "universal veil" (blematogen layer) and primary universal veil.—When the annular gill cavity is formed in *Agaricus*, it separates from the stem at this point, the fundament of the marginal, or partial veil. Since the universal veil or blematogen layer at this stage of development envelops the young carpophore, the question arises as to the relation existing between marginal or partial veil and the universal veil. Is the marginal veil merely a section of the universal veil as Fayod states, or is it a structure partly *sui generis*, and partly consisting of the universal veil which is external at this region? These questions are difficult to answer precisely, since the universal veil, or blematogen layer, in the genus *Agaricus*, and in a number of other genera, is never clearly differentiated in structure from the carpophore as it is in the Amanitae. The delicate, floccose, loose scales sometimes present on the expanding and mature plants as shown in *Agaricus campestris*,[14] may be regarded as the primary universal veil, the *protoblema*, or *protoblem*.[15] Beneath this primary veil or protoblem, in the young carpophore of *Agaricus campestris*, is the zone of loose-meshed tissue homologous with the undifferentiated universal veil, or blematogen layer in *Agaricus arvensis*, *Ag. comtulus*, and in *Amanitopsis vaginata* just described. But since, in these species of *Agaricus*, no distinct cuticle or cortex of the pileus of a definite cellular structure, markedly different from that of the blematogen is developed, which releases the universal veil as is said to be the

[13] *βλημα* = cover; *γενής* = producing.

[14] See Plate 10, and Plate 12, figure 18, in Atkinson, Geo. F. The development of *Agaricus campestris*. Bot. Gaz. **42**: 241–264. *pls. 7–12.* 1906.

[15] *πρῶτος* = first; *βλημα* = cover.

case in Fayod's angiocarpous type (l. c., p. 286), nor is released by the gelatinization of an intermediate zone as in the *Amanitae*, it may have no very great taxonomic significance. It is fundamental tissue of limited extent, the outer layers are often gradually and irregularly broken down and partly exfoliated as the plant matures. Where it is quite distinct at maturity there occurs considerable increase of its elements during early stages of growth. An inner zone, or in some cases perhaps nearly all of it, remains in coalescence with the undifferentiated surface of the pileus. But when it is of the character presented by *Agaricus arvensis* (figures 1–4) and *comtulus* (figures 7 and 10), consisting of thick-walled hyphae, further growth of its elements is probably not extensive. In such cases the outer portion is sloughed off or exfoliated as shown in figures 5, 6 and 9, leaving the surface of the young pileus more or less eroded for a time from an irregular cleavage plane through the zone of the universal veil.

Since no definite boundary between the universal veil and pileus can be found in these examples, it appears to me, that, in the genus *Agaricus*, the external fundamental tissue below the pileus fundament is not always separated from the fundament of the partial veil, but gradually passes over into it, so that the partial veil really has a duplex structure at a very early stage, different from the duplex condition which appears later due to growth from the margin of the pileus and from the surface of the stem. The innermost portion of it is continuous with the margin of the pileus tissue from a very early stage. Further development of this fundamental tissue, forming the marginal veil, takes place after its separation from the stem primordium by the annular gill cavity. The inner portion of it is also increased by continuation of the growth of threads from the margin of the pileus which seems to indicate rather clearly that the marginal or partial veil is not wholly made up of a section of the universal veil.

The "universal veil," or blematogen layer, then, in the species of *Agaricus* thus far studied by myself, one might say consists of a poorly defined external zone of fundamental tissue, not clearly differentiated even after the organization of the pileus, so that the inner portion is more or less concrete with the pileus and marginal veil, while the outer portion may entirely disappear or remain as loose fragments or delicate scales on the surface of the pileus, forming in some cases a slight external contingent of the marginal veil.

Where the external free contingent of the primary universal veil,

or protoblem, is abundant, a distinct, though slight annulus may be formed at the base of the stem. This I have observed a few times in the case of *Agaricus campestris*.

Smith figures diagrammatically the structure of *Agaricus campestris*.[16] Since there is no discussion of the morphological characters of *Agaricus* it is difficult to understand what his conception is of the universal veil and marginal veil in this genus. He figures a universal veil (U.V.) which extends from the base of the stem up over the entire carpophore and also a small ring at the base of the stem as the lower remnant of the universal veil after expansion of the plant. In addition to this an inner veil, the partial veil is illustrated as a distinct structure which forms the annulus. In his diagnosis of *Psalliota* (l. c., p. 170), he says: "Veil universal, concrete with the cuticle of the pileus and forming an annulus on the stem." The annulus which he figures from the universal veil is at the base of the stem while the structure marked annulus (A.N.) is midway on the stem. In his characterization of the family *Agaricaceae* (l. c., p. 11) he clearly distinguishes between the "*primary or universal veil*" which forms the volva and fragments on the pileus, and the partial veil. "In some species a *secondary* or *partial* veil is also present in the earlier stages spreading from the upper part of the stem to the edge of the pileus. This veil is finally ruptured and partly persists as a ring or annulus (A) encircling the stem."

Cooke[17] says in his characterization of *Psalliota* (*Agaricus*), "Veil universal, concrete with the cuticle of the pileus, and fixed to the stem, forming a ring." In his Tribe *Psalliota* Fries[18] says "veil annuliform, subpersistent, strictly speaking partial," and adds that a rudiment of a subuniversal veil is present in some species among which is *Ag. campestris*. This "subuniversal veil" is probably what I have here termed the primary "universal veil," or protoblem. It appears that some authors regard the partial veil in *Agaricus* and some other genera merely as a part of the "universal veil," while others regard it as a distinct structure.

It does not seem worth while to inquire further into the literature, which is purely systematic, for the characterizations given are, in general, not based on studies of development from very young stages.

[16] Smith, W. G. Synopsis of the British Basidiomycetes, fig. 42. 1908.

[17] Cooke, M. C. Handbook of British Fungi **1**: 136, 137. 1871.

[18] Fries, E. Syst. Myc. **1**: 280. 1821. "*velum annuliforme, subpersistens, proprie partiale.*"

Comparison with Lepiota.—It is worthy of note, however, that while several authors since Fries' time have stated that in *Agaricus* (*Psalliota*) the "universal veil" is concrete[19] with the cuticle of the pileus, Fries used this expression only in connection with his Tribe *Lepiota*.[20] Studies on the development of species of *Lepiota* may throw some light on the relation of the universal veil and partial veil in forms where the "universal veil" is not clearly separated from the pileus. I have studied the early stages of development in *Lepiota clypeolaria* and find a well-formed external layer, duplex in structure enveloping the entire carpophore except the extreme base. This may well be considered a "universal veil" or the fundament of one, a *blematogen layer* which does not become separated from the pileus. The portion of the partial veil lying between the margin of the young pileus and stem is differentiated later, and although the universal and partial veils never become clearly separated from each other, the position and structure of the universal veil is so characteristic in the young stages, that it seems reasonable from a purely morphological standpoint to recognize a "universal veil," or blematogen layer, and, in addition, a partial veil. A full account of these studies on *Lepiota clypeolaria* will be published in another paper.

In the species of *Agaricus* here considered, the structure which may be regarded as representing the "universal veil," or blematogen layer, is far less distinct than it is in *Lepiota clypeolaria*, though clearly as distinct as it is in the young carpophore of *Amanitopsis vaginata*. But since there is a poorly defined external layer of the fundamental tissue lying outside of the more or less parallel, radiately arranged hyphae which organize the surface or cuticle of the pileus, though not clearly separated from it, we may consider this layer as homologous with the "universal veil," a blematogen layer in *Agaricus* also. As interpreted here it is a thin layer covering the young pileus and partial veil. In the very young carpophores it is rather thick and prominent in comparison with the fundaments of pileus and stem. As the expansion of the young plant takes place the outer portion of it is torn into fragments which may be so scant as to be unrecognizable, or disappears, or may appear as small patches on the pileus. Some of the inner portion may remain in close connection with the surface of the pileus,

[19] See Cooke, M. C. Handbook of British Fungi, 136, 137. Fayod, V. Ann. Sci. Nat. Bot. VII, **9**: 181–411. *pls. 6, 7.* 1889.

[20] Syst. Myc. **1**: 19. 1821.

and may be said therefore, to be concrete with it. But the evidence of the presence of a "universal veil" and its relation to the pileus is not so clear as in *Lepiota clypeolaria*.

Comparison with the Amanitae.—In the Amanitae, "the universal veil," quite prominent even in the young carpophores, is still not precisely differentiated in *Amanitopsis vaginata*,[21] not more so than in the young carpophores of *Agaricus arvensis* and *Ag. comtulus*.

When the pileus surface is quite well organized in the *Amanitae* there is a zone of parallel hyphae between the pileus and universal veil which gelatinizes, or disintegrates in other ways, and separates the universal veil[22] clearly from the pileus. The position of the partial veil in the *Amanitae* is such that at no time is there any question as to its distinctness from the "universal veil," though the fundamental tissue from which it originates is in contact with that of the universal veil at an early stage of the carpophore. It must be remembered that in the primordium of the carpophore, the fundamental tissue, from which all parts of the plant arise, is continuous and undifferentiable, but this does not mean that when organized the stem is to be considered a part of the pileus.

Is there a primary universal veil, or protoblem, in A. arvensis and Ag. comtulus?—It is quite possible that, in the very young carpophores of *Agaricus arvensis* and *Ag. comtulus*, there is a primary universal veil, or protoblem, as in *Agaricus campestris*, and that it is represented in part by the thin exfoliated portions shown in figures 5, 6, 7, and 10. But in carpophores developing underneath the substratum, as these were, it is difficult to determine this point with precision. In specimens artificially grown, where the carpophores are exposed from a very young stage, as is often the case with *Agaricus campestris* in culture, it should not be a difficult question to settle.

Double margin of the partial veil.—In *Agaricus* as epinastic growth inrolls the margin of the pileus, the increase of the fundamental tissue of the partial veil often covers the external surface of the inrolled pileus margin. In such cases, as the pileus expands and the margin separates from the edge of the partial veil, the latter presents two edges. When the veil is quite tumid and not broad, and the margin of the pileus is very thick as in *Agaricus campestris* var. *edulis*,[23] or in

[21] The development of *Amanitopsis vaginata* will be published in another paper.

[22] Now a *complete* or *finished veil*, or *teleoblema* (τελειος = complete or finished, βλημα = cover).

[23] Vittadini, G. Fung. Mang. 41. *pl. 6.* 1835.

Agaricus rodmani Peck[24] (which may be identical with the variety *edulis*), the annulus has a double edge. Since the lower edge slips off from the under surface of the pileus margin, it might be regarded by some as a volva. But in robust specimens of *Agaricus campestris* where the double margin of the annulus is often marked, there is frequently, in addition, a delicate ring at the base of the stem, the lower remnant of the primary universal veil or protoblem. The annulus with its duplex edge is situated above the base of the stem, and its lower limb is separated from the surface of the stem during expansion. These two facts in connection with what is known as to the considerable increase of the fundamental tissue from which the partial veil originates, argue against the volva nature of the lower limb of such an annulus, and also speak in favor of regarding the partial veil of *Agaricus* as distinct from the "universal veil" and not merely a section of it.

SUMMARY

1. In *Agaricus arvensis* the very young carpophores show an internal differentiation into a pileus and stem primordium, the pileus primordium appearing as a small rounded projection from the broad stem primordium, and there is a very slight constriction at the point of junction of the two. At the point of constriction the fundamental tissue presents a more open mesh indicating the tension from expansion of the surrounding parts which eventually forms the annular gill cavity. The fundaments of the pileus and stem at this stage stain faintly in contrast with the deep stain of the surrounding fundamental tissue. Nevertheless there can be discerned at the lower margin of the pileus fundament, just above the point where the annular gill cavity is to be formed, a small area of compact parallel hypae which form the fundament of the hymenophore and pileus margin.

2. Enveloping the primordia of the stem and pileus is a zone of fundamental tissue. The walls of the hyphae are thicker than those of the pileus and stem fundaments, and stain deeply but the mesh is more open. An outer, ill-definable zone of this represents the "universal veil," or blematogen layer, homologous with a similar layer in *Amanitopsis vaginata*.

3. The outline of the annular gill cavity, and the young hymenophore during the early stages, rises outwardly at an oblique angle from

[24] 48th Rept. N. Y. State Mus. Nat. Hist. 137. 1897.

the stem. But later as the epinastic growth of the pileus becomes stronger, and the stem begins to elongate, the direction becomes reversed, and the outline of the gill cavity and the hymenophore extends outward and downward.

4. Distinct organization in the pileus first appears at the margin, indicated by the parallel growth of the hyphae, under the influence of epinasty. The surface of the pileus proper can here be distinguished from the external, intricately interwoven fundamental tissue which constitutes the "universal veil," or blematogen layer.

5. Stem organization can be observed in the more deeply staining portions of the stem fundament, as growth continues. At first it is broader than long, the outline of the stem cortex staining more deeply.

6. The marginal, or partial, veil is first differentiated by the appearance of the annular gill furrow. It extends from the margin of the pileus to near the base of the stem, and is covered externally by the "universal veil," usually with no well-formed line of demarcation between the two structures. The tissue of the partial veil increases greatly by growth of this inner fundamental tissue, by growth also from the margin of the pileus, which forms a part of the inner (upper) more dense portion of the veil. Abundant increase occurs also next the stem on the lower (outer) side of the partial veil. Thus is formed a duplex partial veil of much looser, more spongy structure below. As the plant expands the partial veil is at first torn from the lower surface of the stem. As it is stretched by the expansion of the pileus the looser, spongy, lower portion of the veil is separated from the pileus margin and surface of the stem and torn into the scales characteristic for the species, while the firmer upper (inner) portion is later separated from the margin of the pileus. In very robust specimens this loose tissue of the under surface of the annulus may be so abundant as to leave many scales on the stem giving it a peronate character.

7. In the very early stages of *Agaricus comtulus*, the first evidence of the differentiation into pileus and stem primordia is a dense, deeply staining, internal, annular area, appearing in longitudinal section as two deeply staining areas symmetrically disposed. This is the primordium of the hymenophore and probably also of the pileus margin. At the same time a less deeply staining dome-shaped area, the margin of which connects with the internal annular hymenophore primordium, or a general central area of larger extent, marks the differentiating pileus primordium. The stem fundament lies below.

8. External to the pileus primordium and the upper portion of the stem fundament is a zone of fundamental tissue with an open mesh. The hyphae in general have a strong radial direction but are clearly interwoven into an open-meshed plectenchyma. The surface is not marked by free ends, but by tangentially lying threads forming part of the weft. The outer portion of this represents the "universal veil," or blematogen layer.

9. The later stages of development are in general as in *Ag. arvensis*, but the partial veil, while presenting the same general duplex character, is not so strongly developed.

10. In all three species of *Agaricus*, which I have studied, there is an external zone of fundamental tissue. The outer portion of this, not well defined, does not pass over into, or give place to, the cuticle proper of the pileus, nor the partial veil. This not well defined outer zone of fundamental tissue represents the "universal veil," or blematogen. An outer portion of the "universal veil" usually becomes torn free because of a lagging or cessation of growth. It may form delicate scales on the pileus, or disappear earlier. An inner portion of the universal veil, variable in amount, remains concrete with the cuticle of the pileus. A small portion in a very young stage lies external to the partial veil and is connected with its outer surface in the young stage. But the great increase in the partial veil, by additions from the margin of the pileus and by growth of the portion next the stem, indicate that the "universal veil" probably plays an insignificant part in the formation of the partial veil, which is a distinct structure.

11. The "universal veil" as interpreted here, is homologous with the undifferentiated "universal veil" in *Amanitopsis vaginata*. Since this zone gives rise, in a later stage of development, to the mature universal veil, or volva, in the *Amanitae*, it may be called a *blematogen layer*, or *blematogen*.

12. In *Agaricus campestris*, under certain conditions, particularly those of culture, there is often manifest an additional universal veil of delicate floccose character, easily separated from the young carpophore, which in age is found as small white floccose patches on the surface of the pileus. This may be called the primary universal veil, or, to be more exact, the *protoblema* or *protoblem*. When present it is external to the *blematogen layer* which, in the species of *Agaricus* studied here, is never differentiated into a distinct universal veil, or *volva*, = the *teleoblema*.

DESCRIPTION OF PLATES I AND II

The photomicrographs were made as follows: Figs. 1–6 with an extension camera and Zeiss lenses, × 15 diameters. Figs. 8–11 were made with a Zeiss microscope, the object being 370 mm. from the sensitive plate; figs. 7, 10 and 16 with ocular no. 4 and objective no. 16 mm.; fig. 8 with ocular no. 8 and objective no. 3 mm.; fig. 9 with ocular no. 12 and objective no. 16 mm.

FIG. 1. Longitudinal section of very young carpophore of *Ag. arvensis* showing earliest origin of gill slits as two symmetrically disposed light spots, separating pileus fundament above from the stem fundament below, indicating a constriction between them. External to the fundament of the pileus and stem is the fundament of the "universal veil," or the blematogen layer. It is easily recognized in this figure by the more open mesh of its tissue compared with the denser tissue of the pileus and stem fundaments, and stains darker because the thick walls of the hyphae take up the stain readily. The base of the young carpophore is lighter colored than the stem fundament indicating that growth is more active in the latter. The rhizomorph is attached to the base.

FIG. 2. Same in a little older stage, the gill slits are evident, the hymenophore primordium is well organized as also the primordium of the pileus margin shown by the deeper stain over the gill slits. Note the oblique position of the gill slits rising outward and upward, also shown in fig. 3.

FIG. 3. Same in a still more advanced stage. The pileus margin is more definite and the inner limit of the blematogen layer is more distinct. The outline of the stem is more distinct showing its present form to be shorter than broad. In figs. 2 and 3 there is shown the exfoliation of a very thin layer from the carpophore. This may represent the primary universal veil, or protoblem, present sometimes on young carpophores of *Ag. campestris* in addition to the blematogen, or it may represent merely a dead outer layer of the blematogen which was in contact with the substratum; it is difficult to determine this point on carpophores developed in the substratum. A similar exfoliating layer is shown in figs. 6 and 10.

FIG. 4 is a section of a young carpophore of *Agaricus arvensis* or a closely related species, collected in the edge of the forests south of Pontarlier in 1905. If it is not *Ag. arvensis* it is probably *Ag. flavescens* Gillet, as young carpophores of this species were collected, but the number became detached. It differs from fig. 1 chiefly in the very deep stain of the hymenophore primordium, and shows also a dome-shaped primordium of the pileus connecting with the primordium of the hymenophore and pileus margin, though not so deeply stained. The blematogen layer is very deeply stained due to the absorption of the stain by the thickened hypha walls. The section was not decolorized to the extent of that of fig. 1, but if it were the primordium of the hymenophore would stand out strongly as compared to that in fig. 1. The reactions here are more like those in specimens of *Ag. campestris* studied.

FIG. 5. Sections of an older stage of *Ag. arvensis* than shown in fig. 3. The position of the gill "slit" is now reversed, sloping downward. The fundaments of the lamellae are beginning to show as low folds. The outline of the surface of the stem is very distinct as a downward and outward sloping dark area below the partial veil. The surface of the primordial pileus is nearly organized, its elements interlacing with the inner layer of the "universal veil," or blematogen which still shows the coarser mesh. The partial, or marginal veil shows a section of the blematogen or

"universal veil," as its outer surface, but the bulk of it is formed by the growth of threads from the margin of the primordial pileus and increase of its own elements. The duplex character is beginning to show, the lower portion showing a more open mesh, increase having come chiefly from growth of fundamental tissue between the blematogen and stem surface.

FIG. 6. Section of a somewhat older carpophore of *Ag. arvensis*, the gill cavity slopes downward still more due to continued epinasty of the pileus margin and the elongation of the stem; the duplex character of the veil is more distinct; the bulb of the carpophore has broadened greatly but has not elongated appreciably so that the stem surface here is horizontal while the main part of the stem is elongating, which brings the surface nearer a perpendicular position. The open mesh character of the medulla is beginning to show due to a lagging behind in growth. The primordial surface of the pileus has become concrete with the inner zone of the blematogen, or "universal veil," so that its outer zone really becomes the surface of the mature pileus.

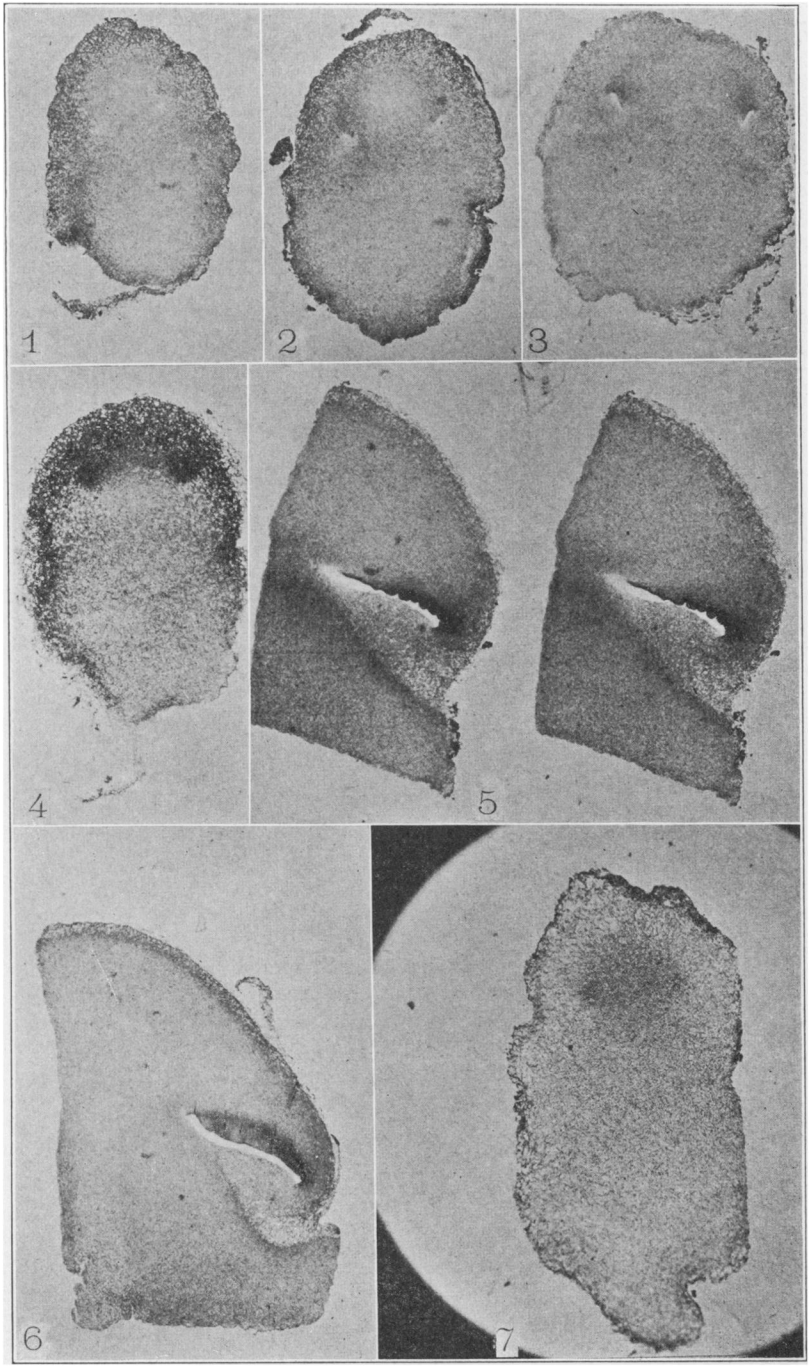
FIG. 7. Section of a young carpophore of *Ag. comtulus* showing in the upper portion the roundish primordial area of the pileus, on either side the more densely staining primordium of the hymenophore and pileus margin; below the nascent primordium of the stem, enveloping stem and pileus fundaments, is the coarse-meshed blematogen, or "universal veil."

FIG. 8. *Ag. arvensis*, highly magnified portion of fig. 1 showing details of structure and differentiation in the region of the early primordium of the hymenophore and pileus margin. This is located at the intersection of lines perpendicular to *a*, *a*. At the right note the coarse-meshed tissue of the blematogen with its thick-walled hyphae, in strong contrast with the dense area at the left with thin-walled hyphae. At the angle of this tissue (intersection of lines from *a*, *a*) note curving downward of the elements of this primordium. The open-meshed tissue beneath is the beginning of the gill cavity, and the threads of this tissue form the primordium of the inner portion of the partial veil; the hyphae are thin-walled and distinct from those of the blematogen lying outside.

FIG. 9. *Ag. arvensis*. Highly magnified portion of a section from the same carpophore as fig. 2, showing young gill "slit," the hymenophore primordium just above; the primordium of the pileus margin above and slightly to the right, at intersection of perpendicular lines from *b*, *b;* on the right the open-meshed tissue of the blematogen, or "universal veil," below the margin of the pileus and the gill "slit" is the now more abundant tissue of the partial veil of finer texture than that of the blematogen.

FIG. 10. *Ag. comtulus*. Section of well advanced carpophore, showing the hymenophore primordium with nascent lamellae; the distinct primordial margin of the pileus, the less differentiated area of the pileus primordium above; the loose meshed blematogen, or "universal veil," the well advanced partial veil of duplex structure below the gill slit covered externally by a section of the blematogen; the conical primordium of the stem below.

FIG. 11. *Ag. comtulus*. Section of a nearly mature carpophore, slightly tangential, showing nearly mature lamellae; duplex partial veil; surface of stem; and pileus surface "concrete" with the "universal veil," or blematogen; a section of the latter forms one-third to one-half the thickness of the portion of the partial veil extending from margin of pileus to its junction with the lower portion.



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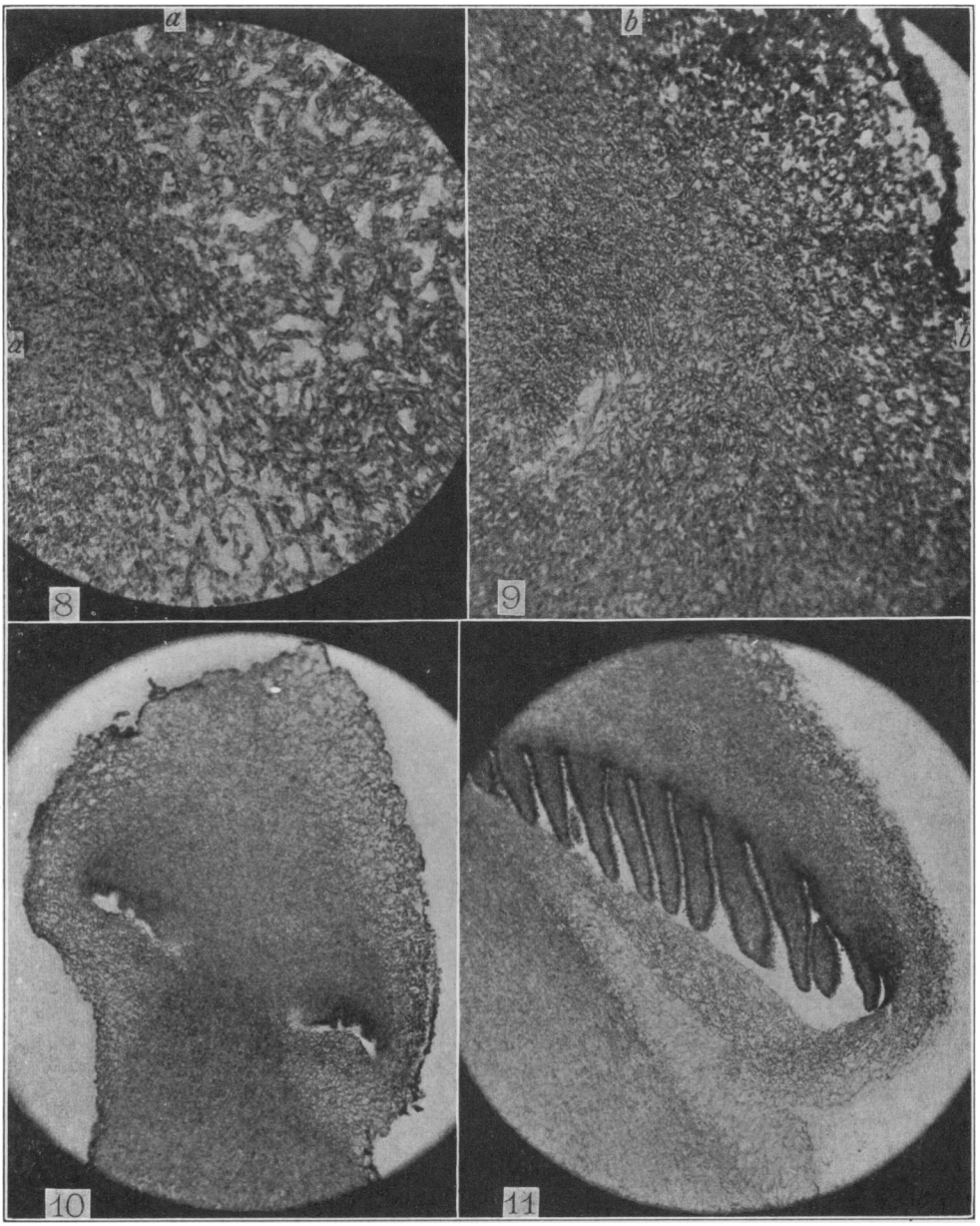

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